NOTES ON THE MACRO-BENTHOS OF KENYAN MANGROVES

by:

Marco Vannini[1]
& Stefano Cannicci[2]

The notes were made for a post-graduate course in "Tropical coast ecology, management and conservation", organised by Free University of Brussels and University of Nairobi, hosted at Kenya Marine and Fisheries Research Institute, with a support by IOC (Gazi, Mombasa, Kenya, July 1997).

Acknowledgements. Many thanks are due to both Maddalena Giuggioli and Gianna Innocenti for their helping in preparing these notes and to Renyson K. Ruwa for his many suggestions during our field work. Most of the pictures (the beautiful ones !) are due to Riccardo Innocenti. Special thanks are due to Dr. E. Okemwa (KMFRI Director) for providing us many facilities during our work in Kenya. Our roads and Kenyan mangroves would probably never have met if one of these roads had not one day crossed Philip's road. For those who have some experience of Kenya coastal ecology, Philip obviously cannot be anybody but Philip Polk, magnanimous spirit and, incidentally, Professor of Ecology at the Free University of Brussels.

MANGROVE TREES

Mangroves is the general name for several species (belonging to different families) of trees (including a palm tree) able to grow in an environment with **2.0-3.8 % of salinity**. **Mangrove** is also the name for the whole trees association ; in this latter case the term **mangal** can also be used (as well as in Portuguese and French).

Mangroves are restricted to **tropical and subtropical areas**, where the average minima are **never lower than about 20°**.

[1] Museum of Zoology, "La Specola", of the University of Florence, via Romana 17, 50125 Florence, (Italy) & Centre of Tropical Faunistics and Ecology of C.N.R., via Romana 17, 50125 Florence (Italy)
tel : ++39 55 2288259 fax : ++39 55 225325, e-mail : vannini_m@dbag.unifi.it

[2] Department of Animal Biology and Genetics, "Leo Pardi", via Romana 17, 50125 Florence (Italy)

The mangrove species to be found in East Africa are :

1. *Avicennia marina* (Forskål)
2. *Bruguiera gymnorhiza* Lamarck
3. *Ceriops tagal* Rob.
4. *Heritiera littoralis* Drymand
5. *Lumnitzera racemosa* Van Steenis
6. *Rhizophora mucronata* Lamarck
7. *Sonneratia alba* Bl.
8. *Xylocarpus granatum* Koenig

The most common species in Kenya are only six : *A. marina* (**AV**), *B. gymnorrhiza* (**BR**), *Ceriops tagal* (**CE**), *L. racemosa* (**LU**), *R. mucronata*(**RH**), *S. alba* (**SO**).

THE MANGROVE ENVIRONMENT

Mangroves grow on intertidal, more or less sheltered, gently sloping flats. Muddy flats are the typical environment for most of the mangroves but sandy flats can also be common. In both cases, the incoherent substratum layer can be quite deep (more than one meter) but often it can also consists of only a few centimetres of sand or muddy-sand, covering a limestone (usually a fossil reef) layer.

Traditionally we can distinguish : 1) **creek mangroves**, 2) **coastal mangroves**, 3) **estuarine mangroves**. Creeks and sinuous estuaries can easily offer the mangroves the protection they need to grow well. The necessary protection to allow mangroves to grow on the exposed coastal line is usually due to favourable local current conditions or else, more often, by a barrier reef or by one or more islands protecting the coast from the ocean winds and waves (see, in Kenya, Shimoni).

MACROBENTHOS SPECIES

A list of mangrove macrobenthic species can include 1) animals permanently found within the mangrove belt (Table I) or else 2) species only occasionally visiting such environment because they are occasionally migrating within it (crabs such as *Portunus pelagicus*) or because they are living in bordering environments, such as the wide bare muddy platforms, bordering the mangrove belt seawards (crabs such as *Eriphia smithi* or *Calappa hepatica*).

If these are the species to be **permanently found within the mangroves**, a further question can arise : which are the species who can **only** be found in mangroves ?

We know that the waves reaching the coast at high tide have a tremendous effect on selecting species (sometimes within the same genus or subfamily) which are able to stand high energy waves or preferring low energy ones. Are the mangroves colonised by any low energy species or is there a typical mangrove fauna, which is obviously also low energy adapted, but somehow strictly depending from that special tree association ?

Bivalves will encrust any hard substratum, no matter if a mangrove root or not. Little is known about *Isognomon dentifer* but *Saccostrea cucullata* does not even discriminate between sheltered and non sheltered environment.

Littorina scabra, within sheltered environment, will climb on any sort of hard substratum, dead trunks, fisherman boats, etc.

Merguia oligodon has been found in (sheltered) environment other than mangroves.

Thalamita crenata has commonly been found in any sort of sheltered environment.

Metopograpsus thukuhar (little is known about the other two congeneric species) can be found on any sort of hard substratum within sheltered areas, including fishing boats.

Sesarma meinerti has been seen to colonise banks bordered by *Casuarina* (Mauritius) or by Mango trees as well (South Somalia)

Ocypode ceratophthalmus is not a typical mangrove species and only appears if suitable sandy areas are available (on upper littoral)

Uca inversa, Uca annulipes and *Uca vocans* do not need to inhabit mangroves but only the right kind of substratum (in the extralittoral, mid and lower littoral, for the three species respectively) and can be found in areas with no mangroves at all.

Dotilla fenestrata is not a typical mangrove species and only appear if suitable muddy-sandy areas are available (on lower littoral).

All the *Macrophthalmus* species only inhabit the muddy platform bordering the mangroves, at a certain distance from the trees themselves, and can thus hardly be considered as mangrove species.

Cardisoma carnifex is known to inhabit private gardens, under *Casuarina* trees in Mauritius, Aldabra and other sites in the Indo-West Pacific.

Table I. Provisional list of the main Kenyan species permanently found in the mangrove belt, i.e. the mangrove macrobenthic fauna, *sensu strictu*.

Echinoderms (Holot.)	
	Hoshimella okemwai (Borri)
Molluscs	
Bivalvia	
	Saccostrea cucullata (Von Born)
	Isognomon dentifer
Gastropoda	
	Terebralia palustris (L.)
	Littorina scabra (L.)
	Cerithidea decollata (L.)
	Cerithium spp.
Crustaceans	
Decapoda	
Natantia	
[illegible]	
	Merguia oligodon (De Man)
Thalassinidea	
	Thalassina anomala (Herbst)
Brachyura	
Xanthoidea	
	Epixanthus dentatus White
	Eurycarcinus natalensis (Krauss)

(follows)

Table I. (follows)

	Portunidae		
			Thalamita crenata H. Milne Edw.
			Scylla serrata (Forskål)
	Grapsidae		
		Grapsinae	
			Metopograpsus messor (Forskål)
			Metopograpsus oceanicus (Jacquinot)
			Metopograpsus thukuhar (Owen)
		Sesarminae	
			Neosarmatium meinerti (De Man)
			Neosarmatium smithi (H. Milne Edw.)
			Selatium brocki (De Man)
			Selatium elongatum (A. Milne Edw.)
			Sesarma guttattum (A. Milne Edw.)
			Sesarma leptosoma (Hilgendorf)
			Sesarma longipes Krauss
	Ocypodidae		
		Ocypodinae	
			Ocypode ceratophthalmus (Pallas)
			Uca gaimardi (H. Milne Edw.)
			Uca inversa (Hoffman)
			Uca annulipes (H. Milne Edw.)
			Uca tetragonon (Herbst)
			Uca urvillei (H. Milne Edw.)
			Uca vocans hesperiae (L.)
		Scopimerinae	
			Dotilla fenestrata Hilgendorf
		Macrophthalminae	
			Macrophthalmus depressus Rüppel
			Macrophthalmus grandidieri A. Milne Edw.
			Macrophthalmus milloti Crosnier
			Macrophthalmus parvimanus Guérin
	Gecarcinidae		
			Cardisoma carnifex (Herbst)
Anomura			
	Diogenidae		
			Clibanarius laevimanus Buitendijk
			Clibanarius longitarsus (De Haan)
	Coenobitidae		
			Coenobita cavipes (Stimpson)
	Porcellanidae		
			Petrolisthes lamarckii (Leach)
Isopoda			
			Sphaeroma terebrans Bate
Cirripedia			
	Balanomorpha		
			Cthamalus dentatus
			Balanus amphiprite Darwin

Coenobita cavipes, occasionally common in mangrove sandy area (upper levels), is known from every sort of coastal non-exposed environment with sand available.

Sphaeroma terebrans is a wood borer isopod. However, it does not feed on wood but bores into any kind of wood (wooden jetties are endangered) in a sheltered area.

Cirripedia, as well as Bivalves, will encrust any hard substratum, no matter if a mangrove root or not.

It appears that all the remaining species can only be found in mangroves or only occasionally out of it but in strict adjacent environments. We have no idea whether such strict association reflects morphological and/or physiological and/or behavioural adaptations or else can be the effect of an expulsion from similar sheltered environments, due to stronger competitors.

The only species feeding on fresh leaves, also well adapted morphologically to the tree climbing style of life (*Sesarma leptosoma* has the walking legs dactylus transformed into short fangs, reminding the spiders and insects leg tips) is the only one where a strict dependence from the mangrove trees seems evident.

MANGROVE MACROBENTHOS BIODIVERSITY

Again, we have detailed comparative data only for East African decapods. A comparison can be made between the number of species recorded in Kenyan and Somalian mangroves and other littoral environments other than mangroves (rocky cliffs, intertidal rocky platforms, sandy beaches, sheltered beaches and estuaries with no mangroves; fig. 1a). Mangrove decapods make up less than 25% of this fauna (14.6% of which comes exclusively from mangroves and 7.5% non-exclusive). Fringing reef and Intertidal exposed rocky platforms are the most diverse littoral environments while sandy beaches are the less diverse. Sheltered beaches, rocky cliffs and mangroves are somewhere in the middle (Fig. 1b).

The moderate biodiversity of mangroves is however accompanied by extremely dense populations and in no other littoral environment is it possible to observe such crowds of crabs like those in mangrove zones invaded by the species of *Uca* or Sesarminae crabs[3].

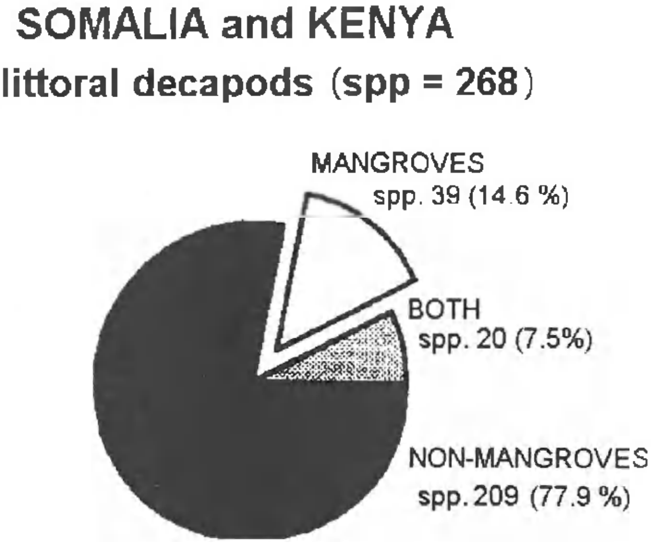


Fig. 1a. A rough representation of the species biodiversity in the Somalian-Kenyan mangroves.

[3] Among molluscs, *Terebralia palustris* can sometimes produce nearly continuous snail "carpets" among the muddy flats and *Cerithidea decollata* can form clusters, around the *Avicennia* trunks, made by hundreds of individuals.

A quantitative evaluation in term of biomass is presently available only in some zones for some fiddler crabs. This is due to both a real lack of studies and to the extreme difficulty in assessing the density of most of the animals other than Ocypodids crabs, which are difficult to excavate and sometimes even to see (*Neosarmatium smithi*).

number of decapod species found in different Somalian littoral environments	**mangrove**	**sheltered intert. flats**	**exposed intert. flats**	**sandy beaches**	**rocky cliffs**	**fringing reef**
shrimps & thalassinids	6	6	19	0	0	49
hermit crabs & Co. (Anomura)	5	4	11	3	8	12
swimming crabs (Portunidae)	8	4	13	0	0	2
xanthids (Xanthoidea)	15	20	39	0	26	58
grapsids (Grapsidae)	14	1	8	0	12	2
ocypodids (Ocypodidae)	13	4	1	5	0	0
majids (Majidae)	0	0	6	0	0	7
other crabs	1	3	10	1	0	6
total	62	42	107	9	46	136

Fig. 1b. A rough estimate of the decapod biodiversity in Somalian littoral environments. Several species found in tidal flats adjacent to mangroves have been here included in the mangrove environment category, over-estimating thus the number of the real mangrove inhabitants *sensu strictu*.

MANGROVE PRODUCTIVITY AND MAIN FOOD-CHAIN

The productivity of mangroves is very high and most of the mangrove output remains "trapped" within the ecosystem itself as dead leaves, dead trunks and roots, and mud. The latter is practically only due to the digestive action of macrobenthic species living mostly or exclusively on dead mangrove leaves and on bacteria and fungi attacking dead wood, animal faeces and, in a lesser extent, dead leaves.

Many macrobenthic species (both among Gastropods and Decapods) are actively feeding on the fallen leaves which are only occasionally able to form a permanent litter. In most of the East African mangroves, the soil thus appears quite bare.

It is interesting to note that the American mangroves food chain is said to be characterised by the role of bacteria directly digesting the dead leaves (which form a consistent mass of permanent litter) while macrobenthic species are mostly only mud eaters.

The **main source of food** for East African macrobenthic species are thus:

1. **Fresh leaves**, directly from the canopy (*Sesarma leptosoma*).
2. **Dead leaves** to be found on the floor (*Terebralia palustris, Cardisoma camifex, Neosarmatium meinerti, N. smithi, Sesarma guttatum*)
3. **Mud.** Some gastropods, young *T. palustris* and most of above species as well as of some of the predators, can feed on mud as an alternative to leaves and preys, respectively.
4. **Micro-algae.** The algal film on hard substrata - leaves, wood trunks, etc.) is exploited by *Littorina scabra* while Ocypodid crabs (*Uca* species, *Dotilla fenestrata*) and other gastropods can remove micro-algae from the mud or sand surface.
5. **Suspended matter** in the water column. Typical filter-feeders are bivalves (such as oysters, *Saccostrea cucullata* and *Isognomon dentifer*), barnacles and Porcellanid crabs (*Petrolisthes lamarckii*).
6. **Dead corps.** Many crabs (*Ocypode ceratophthalmus, Thalamita crenata*, the three *Metopograpsus* species, several Sesarminae species, *Ocypode ceratophthalmus*) and gastropods (*Nassarius* spp.) are scavengers, even if any crabs can be considered mainly so.
7. **Preys.** Some gastropods (Neogastropoda) are preying on other molluscs and several crabs are known to be predators: opportunistic (such as *Metopograpsus* spp., *T. crenata*) or obliged (or nearly so, such as *Epixanthus dentatus, Eurycarcinus natalensis, Scylla serrata*)

FEEDING SPECIALIZATION OF DECAPODS

As illustrated in the previous section, mangrove decapods range from suspension feeders to predators. Opportunistic feeding is probably dominant (Fig. 2) and many species which apparently feed only on leaves (*Neosarmatium meinerti*) and mud (*Sesarma guttatum*) may also prey on a small *Uca* if this comes too close.

On the other hand, according to stomach content (Fig. 2) only *Eurycarcinus natalensis* seems to avoid all vegetable matter while *Thalamita crenata* and especially *Metopograpsus thukuhar* mostly eat algae, while waiting for juicier prey.

The predatory relationships involving Kenyan mangrove decapods is far from being simple (Fig. 3). However one pattern is evident: among obligatory or occasional predators there is no evidence of prey specialisation.

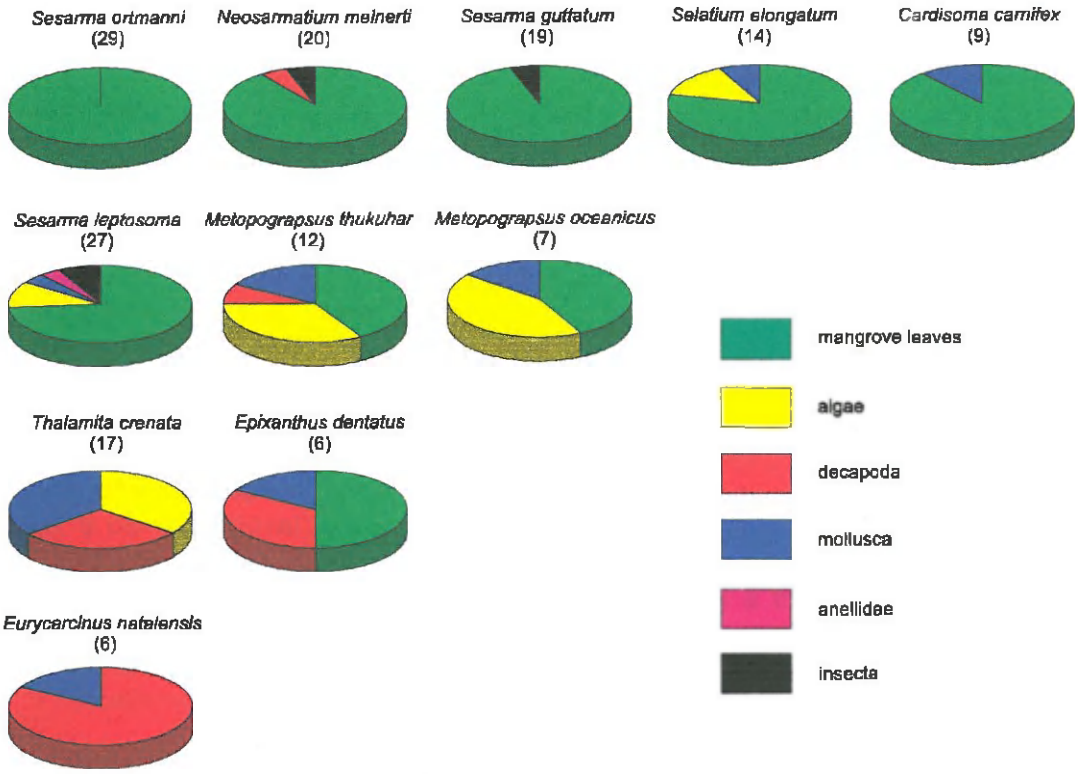


Fig. 2. Stomach content of the main Kenyan mangrove non-ocypodid decapods (in brackets, sample size).

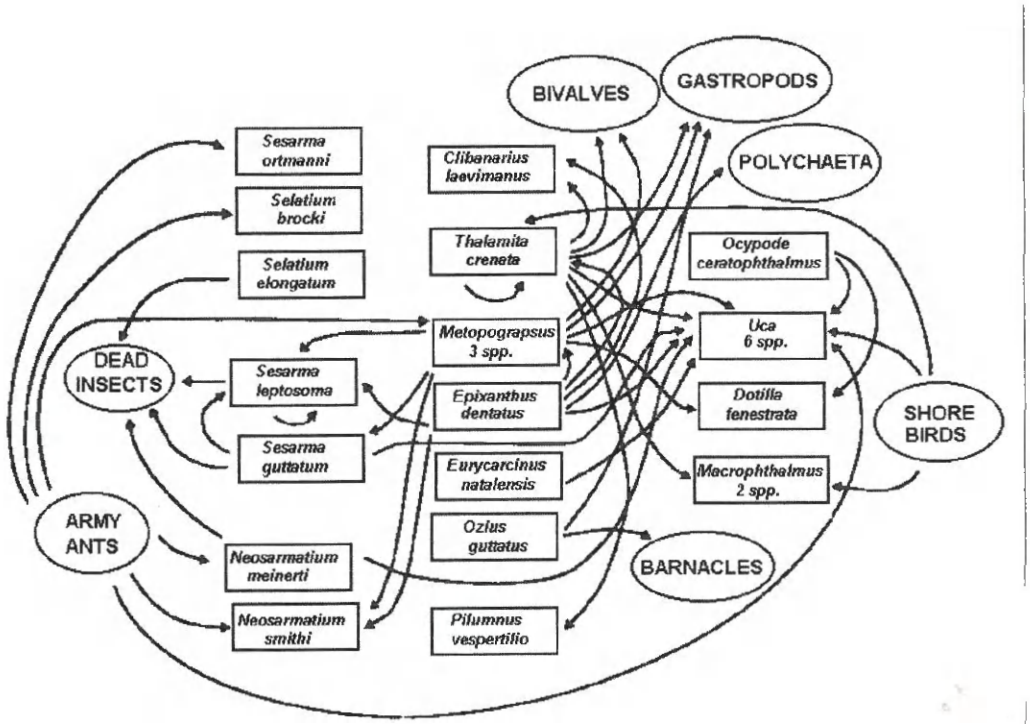


Fig. 3. Predatory relationships of mangrove decapods (including accessory species). Predation direction is indicated but not its frequency since the all predation acts (239) were recorded irregularly and with different techniques (stomach content, direct observations, etc.).

MANGROVES ZONATION

The tree species distribution within each mangrove site, follows a zonation pattern depending from the immersion time i.e., from their vertical distance from the sea water level[4].

Basically, we can distinguish :

1. an **extra-littoral zone** (only reached by the water during EHWST) where LU can be found and the most landwards AV appear,
2. an **upper-littoral zone**, between HWST and HWNT, where AV is the dominating species (with some BR),
3. a **central-littoral zone**, between HWNT and MSL, where RH and CE, (alone or together) are the commonest species,
4. a **seaward fringe**, where a few (but sometimes a thick belt of) SO, protect the RH mass. On coastal exposed mangroves, the SO fringe is to only to be found while in very protected localities, only few scattered SOs can (hardly) be found.

The sixth species, BR, can occasionally be found between zones 2 and 3, sometimes as a dense association, more often, in Kenya, in form of scattered trees.

In Kenya, the two most evident zones usually seen in most of the cases are : an **upper littoral belt rich of AV** and a **central belt with RH** alone **or**, more often, **a mixed RH-CE** association.

If the coast is regularly sloping seawards the vertical zonation will also correspond to a horizontal zonation, with LU, AV, RH and SO, appearing in turn, from land to sea. We have to remember anyway that trees are producing their own soil and the action of digging organisms (especially of Thalassinids) is also responsible for occasional soil rising. On the other hand, the several irregular and sinuous exhaling channels through the mangrove thick can heavily erode the soil (in addition to the action of the main freshwater stream, in the case of estuarine mangroves).

---

[4] The main sea levels, following the commonest terminology, are: **HWST**, level of the average High Waters of Spring Tides ; **LWST**, level of the average Low Waters of Spring Tides ; **HWNT**, level of the average High Waters of Neap Tides ; **LWNT**, level of the average Low Waters of Neap Tides ; **MSL**, Mean Sea Level (the average between LWST and HWST) ; **EHWST**, level of the Extreme High Waters of Spring Tides ; **ELWST**, level of the Extreme Low Waters of Spring Tides (extreme Spring Tides occur close to the springtime and autumn equinoctial).

The *datum* (level 0) of the Tide Tables, does not correspond the MSL but (roughly) to the LWST. During ELWST negative levels can thus recorded. The whole excursion (between the LW to HW levels) at ST, in East Africa, is usually nearly twice as wide as at NT.

Spring Tides (ST) and Neap Tides (NT) are told the tides occurring at Full or New Moon (the former), ad at the first and second quarter (the latter). No relevant difference occur between the Full and New Moon STs. On the contrary, a difference will be constantly recorded between the two tides occurring within the same day (*diurnal disparity*).

As results of all these actions, a mangrove explorer will often record, at low tide, an irregular succession of AV, RH, CE and BR patches, with no relationship at all with their distance from the sea. Only at the beginning of the high tide our explorer will see that, no matter where the RH patch is, this will be always be flooded at least one hour in advance than most of the AV patches and SO patches will always be the first to be reached by the sea water.

MACROBENTHOS ZONATION

Just like across any intertidal environment a zonation pattern can be seen among the different macrobenthic species : extralittoral species are followed by more frankly intertidal ones and among these, some species will concentrate on the upper littoral and others on the lower littoral zones. If this pattern can easily be recognised among sessile animals, it is sometime difficult to be assessed among highly mobile animals such as, for instance, swimming crabs.

It has been suggested that among intertidal non-sessile animals, **iso-zonal** species can be separated from **iso-phasic** ones. The former always remain within the same zone, hiding themselves during the unsuitable respiratory phase. The latter, on the contrary are always exploiting the same respiratory phase and thus migrate land-seawards, according to the tide.

Iso-phasic marine animals such as *Arothron* spp. (porcupine fish), or iso-phasic terrestrial animals such as the lizard *Ablepharus* spp. (on rocky shores, fig. 4), and *Emerita* spp. and *Thalorchestia mertensi* (on sandy beaches, fig. 5), all move landwards during flood tides and seawards during ebb.

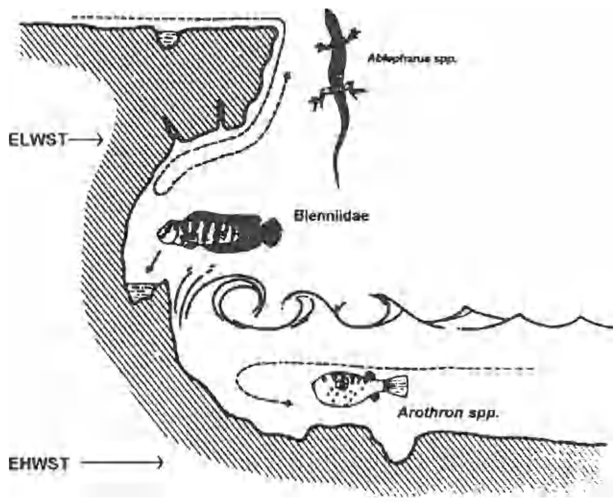


Fig. 4. Rocky cliff. **Iso-phasic** animals : these move with the tide and always remain in the same respiratory phase by adopting the adequate migration. Thus *Ablepharus* spp., a reptile, and *Arothron* spp, a fish, will, in turn occupy the same space. **Iso-zonal** animals : these species, on the contrary, do not migrate but simply hide themselves during the non-suitable phase. Intertidal blennids never abandon their home, and are active only at low tide, when they forage within the little pool they permanently occupy.

Iso-zonal marine animals such as Blennids (on rocky shores, Fig. 4) or *Thalamita crenata* (the common swimming crab living intertidal muddy flats) always remain near their refuge, swimming around, looking for mates and food, during part of the high tide (the latter) or at low tide (the former) and hide themselves within their den, during the opposite tidal phase. On sandy beaches, iso-zonal crustaceans such as *Excirolana* (isopods) are freely wandering around at high tide but disappear within their burrow, at low tide, while crabs such as *Dotilla* (Fig. 5) and *Uca* behave just in the other way round, active at low tide and hiding in their burrow the whole high tide through.

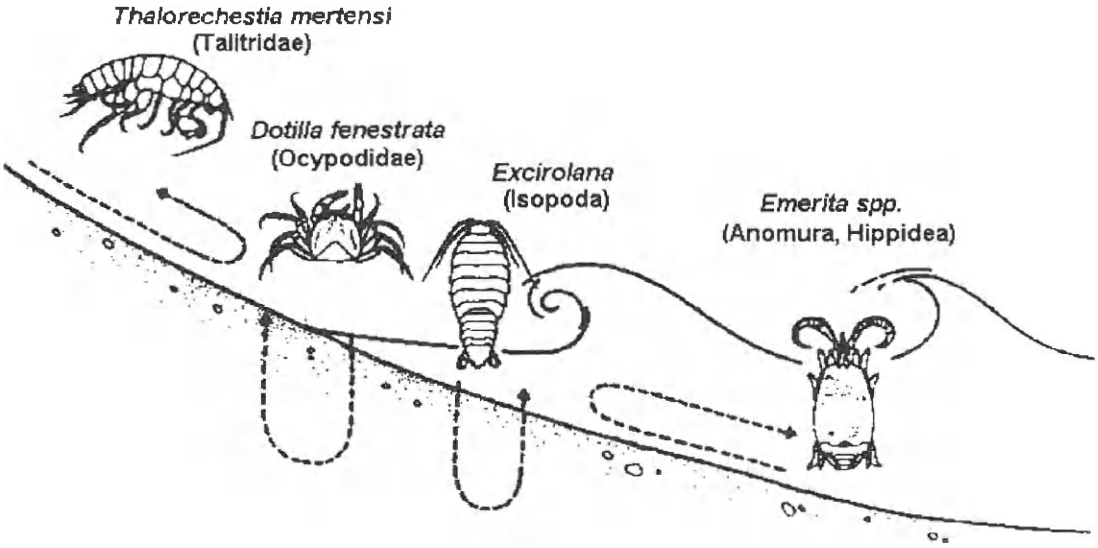


Fig. 5. Sandy beach. Sand-hoppers (Talitridae) and mole-crabs (*Emerita* spp.) regularly migrate and thus always remain, respectively, in the air or in the water (**iso-phasic strategy**). Isopods and ocypodids will, on the contrary, emerge or hide themselves when the beach is, respectively, uncovered or covered by water (**iso-zonal strategy**).

Since both mangrove and macrobenthos zonation probably depend on the immersion time of the different zones, a correlation between the two zonation patterns is often quite evident (Fig. 6). Within the same crustacean subfamily (Sesarminae), the upper *Avicennia* zone is inhabited by *Sesarma ortmanni* and *Neosarmatium meinerti*, the lower *Rhizophora-Ceriops* by *Neosarmatium smithi*, *Sesarma guttatum* and *Sesarma leptosoma*, and the lower seaward mangrove edge, where *Sonneratia alba* is usually most common, by *Selatium elongatum*.

The same pattern can be found within the *Uca* genus where, for instance, *Uca inversa* is very common at the upper edge of the *Avicennia* zone, *Uca annulipes* is the commonest species among most of the lower *Avicennia* zone, *Uca chlorophthalmus* dominates the intermediate zones and *Uca vocans* is typical of the lower levels.

A strict animal-plant relationship has never been found. *Neosarmatium meinerti* can also feed on all sorts of dead mangrove leaves while *Sesarma leptosoma* has been found feeding on fresh leaves of *Rhizophora mucronata, Bruguiera gymnorhiza,* and *Ceriops tagal.*

The gastropod *Terebralia palustris* spontaneously eats, apparently without any special preference, both dead leaves[5] and propagules of *Rhizophora mucronata* and *Ceriops tagal*. Feeding preference experiments on *Cardisoma carnifex* and *Neosarmatium meinerti* have shown a slight preference for *Sonneratia alba* leaves, which is the one mangrove species that both the above two crabs never have the occasion to meet !

1) *Cardisoma carnifex*
2) *Sesarma ortmanni*
3) *Neosarmatium meinerti*
4) *Sesarma guttatum*
5) *Metopograpsus thukuhar*
6) *Metopograpsus oceanicus*
7) *Sesarma leptosoma*
8) *Selatium elongatum*
9) *Epixanthus dentatus*
10) *Eurycarcinus natalensis*
11) *Thalamita crenata*

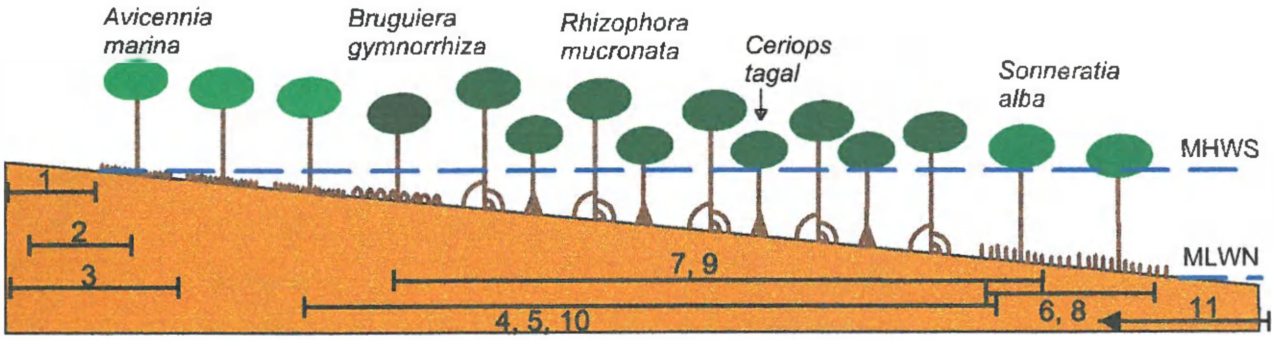


Fig. 6. Schematic pattern of zonation of the main mangrove trees and non-ocypodid decapods species in a Kenyan mangrove.

TIME PATTERNS

Little is known about the activity patterns of mangrove gastropods. Traditionally, mangrove decapods are supposed to be active mainly during the day and at low tide. This idea comes from the many studies on *Uca* crabs which in fact are mostly active during diurnal low tides. However, new findings on the activity of mangrove decapods other than *Uca* seem to indicate the existence of day, night, LT, and HT combined activity patterns (Fig. 7).

The general purpose of such complex activity patterns is probably in a reduction of inter-specific space competition, or else, in an optimal 24 hr environment exploitation by different species in different ways.

It is also interesting to observe that, even within a single species, the individuals are rarely all active at the same time. Again, detailed quantitative information on littoral fauna is very rare, especially for mangrove fauna. However, in many species, more individuals are commonly visible at ST than at NT.

[5] *Terebralia palustris* is also found of fresh mangrove leaves, when available.

The density increase at ST can obviously be due to an increase in the number of active animals at ST. However, an alternative hypothesis is that all the animals may be active, at the same time, during their suitable tidal phase, at ST, while, at NT, they may still all be active but for shorter periods not in phase with each other. Little research has been done on this subject and we do not know much about it.

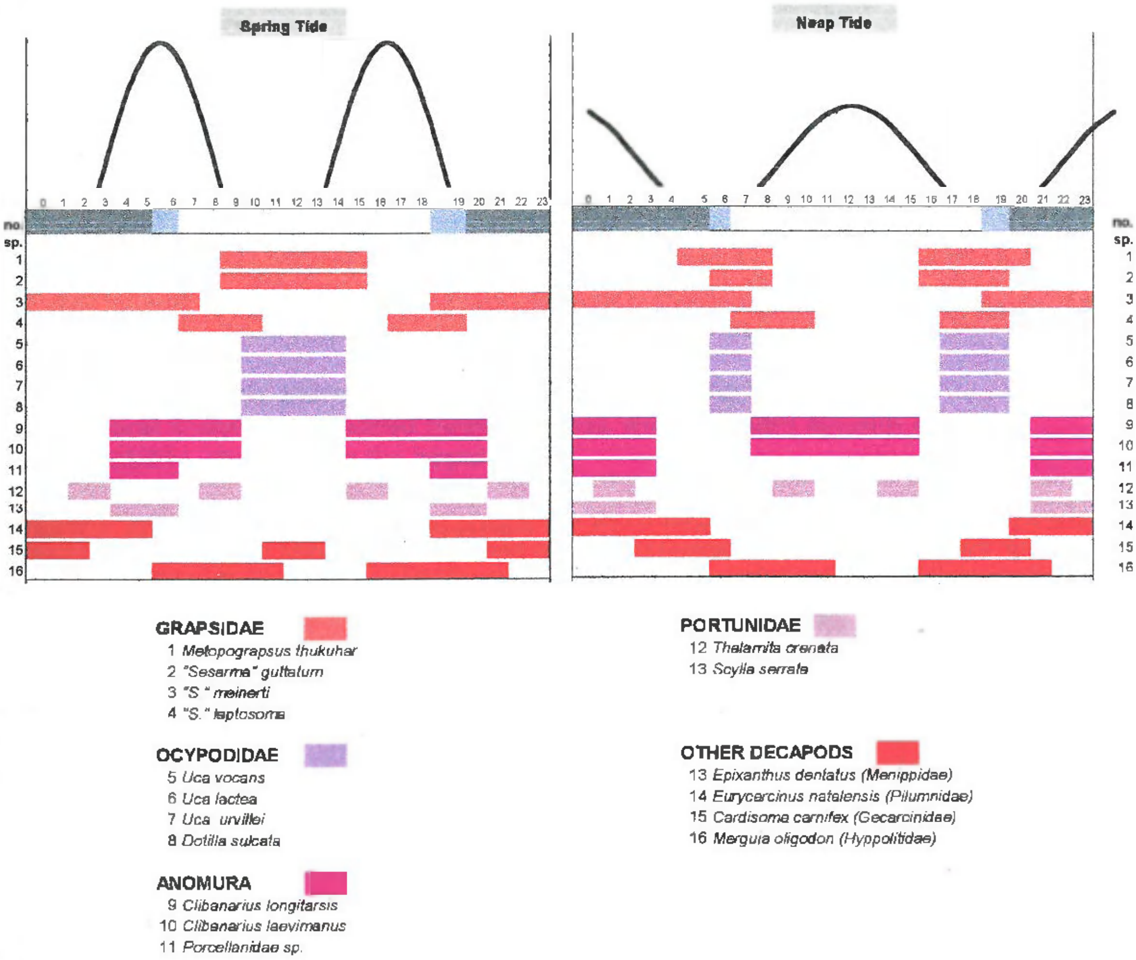


Fig. 7. Main pattern of locomotor activity in 16 species of mangrove decapods in Kenya. Coloured bars, high activity ; no bars, low activity.

REPRODUCTIVE CYCLES

A periodicity in reproductive activity is known for most intertidal organisms but little is known, at least in a systematic way, for mangrove organisms. Many *Uca* species are known to spawn once every lunar month (about 29.4 days) but the since females are not all synchronised they are seen to spawn at each ST. More terrestrial species such as *Cardisoma carnifex* spawn only once or perhaps twice a year, during the highest equinoctial STs. Spawning at ST is probably due to the maximisation of egg exportation since the strongest exhalant (ebb-tide) tidal currents can be recorded in that period.

APPENDIX

SAMPLING

Whatever the goal of an ecological survey may be (the study of a biotope, of species association, of a species population, patterns of zonation, etc.) our recording technique will never be able to deal with the whole set of data behind that biotope, association or population.

The only things we can do are:

1. to "**extract**" a limited amount of data (a "**sample**") from the whole set of data ("**universe**" or "**population**"[6]),
2. to **determine some measures** of the sample (central tendency, variability, etc.),
3. to **infer**, from the above sample measures (by applying the appropriate statistical analysis), the **related measures that, with a certain amount of probability, characterise the population.**

Sampling, measuring and statistical inference are three steps each of them equally important. A weak approach to any of the above procedure will weaken irreversibly the remaining two. In particular we have to remember that a clearer sampling procedure will greatly facilitate measuring and final analysis while no statistical test have been invented yet which is able to cope with poor sampling.

Let us imagine to extract a certain number of samples i.e., by measuring a species density within 9 different mangrove plots, 3 for each of the main AV, RH and SO zones. We will thus have 9 density values, probably quite different from each other. An average density can be calculated (**mean**) as well as the estimate of how the single values vary around the above mean (**standard deviation** = **s** = **SD**).

The two main questions we can now raise are:

1. Why are not all samples identical, or else, why are they variable ?
2. Which is the relationships between the computed samples mean and the "real" mean of the whole population the samples have been extracted from ?

The answers :

1. The samples are variable because :
   a) small variations in the sampling procedure, manual errors, measurement errors, data transcription errors,
   b) ecological variability : small variations in the soil structure (in spite of the apparent soil uniformity, digging may be a little easier somewhere then somewhere else) ; intra-specific biological variability (some crabs are more tolerant of his neighbours than others).

---

[6] ATTENTION ! The term *population* is here used in statistical sense (*statistical population*) and can only occasionally correspond to the concept of population (*genetic population*) as used in genetics and evolutionary biology.

c) the 9 plots we have been physically removing the crabs from, have some relevant difference in their inundation time and/or soil structure and/or resource availability and/or sun exposure.

Causes **a**, **b** and **c** are known to add their effect on the whole variability. Causes **a** and **b** are trivial ones (they are also called **error** or **noise**) and we are not directly interested in them (we only have to try to reduce them to a minimum). Causes **c** (the **signal**) are the ones we intend to study. In other terms, we will try to relate some of the observed differences between samples to possible difference in inundation time and/or food availability and/or sun exposure, etc.

How is this possible ? Let us compare the variability of the three averages for each zone (**between-zones variance**) with the average between the three variability measures for each zone (**within-zone variance**). If the *between* variance is greater than the *within* one, the recorded difference between samples cannot be attributed to causes **a** and **b** alone: some systematic difference (due to some type **c** cause) must exist between our zones (i.e. our crab prefers the upper intertidal level and thus is much commoner within the AV plots). On the other hand, if the *between* and *within* variance are very similar, there is no reason to assume that **a** and **b** causes alone may not be able to explain for the slight differences of that crab density that have been recorded within the different AV, RH or SO zones.

ANOVA test (in its various applications) is the basic test able to statistically evaluate the ratio between the between- and within-samples variance (parameter **F**).

As we can deduce from this simple approach, the possibility of revealing differences between zones in the density of a certain species (i.e., to reach a significance level of parameter F) depends on the low variability of the effects due to causes **a** and **b** as well as on the amount of difference due to **c** causes. The latter are the ones we intend to study and are usually out of our control. The former (**a** and **b**) have to be carefully reduced by standardising the recording techniques, avoiding even the smallest recording errors, checking the homogeneity of the single plots within each zone. The error reduction (or else the enhancement of the **signal/noise ratio**) is the key point in extracting as much information as possible from the samples !

2. One may also wish to define which is the **real** density, for that crab species, for each of the three mangrove zones. In other terms, which is the density that we may find if we could sample the whole *statistical population* (i.e. counting all the crabs, for that species, within the whole AV, RH and SO surfaces of a whole mangrove swamp).

The *real* density will obviously never be assessed. The only thing we can do, on the base of our sampling results, is to define an interval (computing the **standard error** = **SE**), within which, the *real* density has a certain probability to occur. The most commonly used interval corresponds to about twice the SE span and the minor probability traditionally accepted is 95% (**95% confidence limit**). The final statement can thus look like: *"since the recorded density average, for our crab species, in our three AV zones, is 1.9 crabs/m^2 and the 95% confidence limits are +/- 0.9 crabs/m^2, we can infer that, with the 95% of probability, the real density of that crab species, within the AV zone, falls between 1.0 and 2.8 crabs/m^2.*

LITERATURE

Cannicci S., F. Dahdouh-Guebas, D. Anyona, and M. Vannini. 1995. Homing in the mangrove swimming crab *Thalamita crenata* (Decapoda, Portunidae). *Ethology* 100 : 242-252.

Cannicci S., S. Ritossa, R. K. Ruwa & M. Vannini, 1995. Tree- fidelity and hole-fidelity in the tree crab *Sesarma leptosoma* (Decapoda, Grapsidae). *J. exp. mar. Biol. Ecol.*, 196: 293-311.

Cannicci S., R. K. Ruwa, S. Ritossa & M. Vannini., 1995. Branch- fidelity in the tree crab *Sesarma leptosoma* (Decapoda, Grapsidae). *J. Zool., Lond.*. 238: 795:801

Crane J., 1975. *Fiddler crabs of the world.* Princeton University Press.

Crosnier A., 1965. Crustacés Décapodes : Grapsidae et Ocypodidae. *Faune de Madagascar* 18 : 1-143.

Dahdouh-Guebas F., M. Giuggioli, A. Oluoch, M. Vannini, and S. Cannicci. A note on feeding habits of non-ocypodid mangrove crabs from Kenya. *Senckenbergiana Biologica* (in press).

Davie P. J. F., 1982. A preliminary checklist of Brachyura (Crustacea: Decapoda) associated with Australian mangrove forests. *Operculum* 5(4): 204-7.

Gherardi F., M. Micheli and M. Vannini, 1990. Movement patterns and dispersal of the hermit crab *Clibanarius longitarsus* in a mangrove swamp. *Mar. Behav. Physiol.*, 16: 209-223.

Gherardi F., M. Vannini, 1992. Hermit crabs in a mangrove swamp: clustering dynamics in *Clibanarius laevimanus. Mar. Behav. Physiol.*, 21: 85-104.

Guinot D., 1967. La faune carcinologique (Crustacea Brachyura) de l'Ocean Indien occidental et de la Mer Rouge. Catalogue, remarques biogéographiques et bibliographie. Reunion de Specialistes C. S. A. sur les Crustacés, Zanzibar, 1964. Mémoires de l'I.F.A.N. 77 (1966): 237-52.

Hartnoll R. G., 1988. Eco-ethology of mangroves. In : *Behavioral adaptation to intertidal life*, Chelazzi, G. and Vannini, M. (Eds.), NATO ASI Series, New York and London: Plenum Press, pp. 477-489.

Hartnoll R. G., 1988. Evolution, systematics, and geographical distribution. In, *Biology of the Land Crabs*, Edited by W. W. Burggren & B. R. McMahon, Cambridge Univ. Press, pp. 6-54.

Hartnoll R. G., 1975. Grapsidae and Ocypodidae (Decapoda: Brachyura) of Tanzania. *J. Zool., Lond.* 177: 305-328.

Icely J. D. and D. A. Jones, 1978. Factors affecting the distribution of the genus Uca (Crustacea: Ocypodidae) on an East African shore. *Estuarine Coastal and Marine Science*, 6: 315-25.

Jones D. A., 1984. Crabs of the mangal ecosystem. In *Hydrobiology of the mangal*, Eds., F. D Por and I. Dor, Junk, The Hague, pp. 89-110.

Macintosh D. J., 1988. The ecology and physiology of decapods of mangrove swamps. *Symposium of the Zoological Society of London*, 59: 315-41.

Macnae W., 1968. A general account of the flora and fauna of mangrove swamps and forests in the Indo-West-Pacific region. *Advances in Marine Biology* , 6: 73-270.

Micheli F., F. Gherardi & M. Vannini, 1991. Feeding and burrowing ecology of two East African mangrove crabs. *Mar. Biol.*, 111: 247-254.

Ruwa R. K., 1990. The effect of habitat complexities created by mangroves on macrofaunal composition in brackish water intertidal zones at the Kenya Coast. *Discovery and Innovation* 2 :49-55.

Ruwa R. K., 1996. Zonation of crabs that burrow or bury in mangrove vegetation soils on the East coast of Africa. In, *East African Ecosystems and their conservation*, edited by T. R. McClanahan & T. P. Young, Oxford Univ. Press, : 101-130.

Ruwa R. K., 1997. Zonation of crabs that burrow or bury in mangrove vegetation soils on the East coast of Africa. In, *Mangrove Ecosystem Case Studies in Latin America and Africa*, edited by B. Kjerfve, L. D. Lacerda & E. S. Diop, UNESCO Technical Papers in Marine Science, :325-338.

Vannini M., S. Cannicci, and R. K. Ruwa. 1995. Effect of light intensity on vertical migrations of the tree crab Sesarma leptosoma (Decapoda, Grapsidae).*J. exp. mar. Biol. Ecol.*, 185: 181-189.

Vannini M., A. Oluoch and R. K. Ruwa, 1997. The tree-climbing crabs of Kenyan mangroves. In, *Mangrove Ecosystem Case Studies in Latin America and Africa*, edited by B. Kjerfve, L. D. Lacerda & E. S. Diop, UNESCO Technical Papers in Marine Science, :325-338.

Vannini M., R. K. Ruwa, 1994. Vertical migrations of the tree crab, *Sesarma leptosoma* (Decapoda, Grapsidae). *Mar. Biol.* 118: 271-278.

Vannini M. and P. Valmori, 1981. Researches on the coast of Somalia. The shore and the dune of Sar Uanle. 30. Grapsidae (Decapoda Brachyura). *Monitore Zool. Ital. NS (Suppl.)* 14(6): 57-101

Vannini M. and P. Valmori, 1981. Researches on the coast of Somalia. The shore and the dune of Sar Uanle. 31. Ocypodidae and Gecarcinidae (Decapoda Brachyura). *Monitore Zool. Ital. NS (Suppl.)* 14(14): 199-226

Vezzosi R., D. Anyona, S. Barbaresi & M. Vannini, 1994. Activity pattern in *Thalamita crenata* (Portunidae, Decapoda): a shaping by the tidal cycle. *Mar. Behav. Physiol.*, Vol. 24, pp. 207-214.

Lumnitzera racemosa, Kenya

Avicennia marina, Kenya

Bruguiera gymnorrhiza, Kenya

Xylocarpus granatum, Kenya

Ceriops tagal, Kenya

Ceriops tagal (upper)
Xylocarpus granatum (lower)

Sonneratia alba (flowers), Kenya

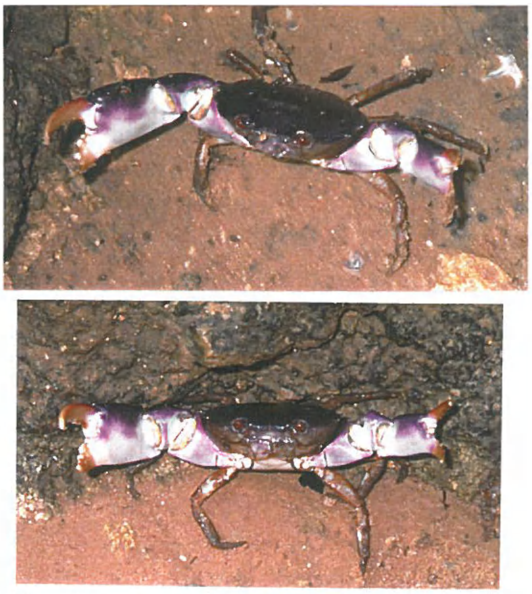
Rhizophora mucronata, Kenya

Ceriops tagal (flowers), Kenya

eriops tagal (propagules), Kenya

encrusting lichens (unknown species)

Loranthus quinquenervis
(Misteltoe)

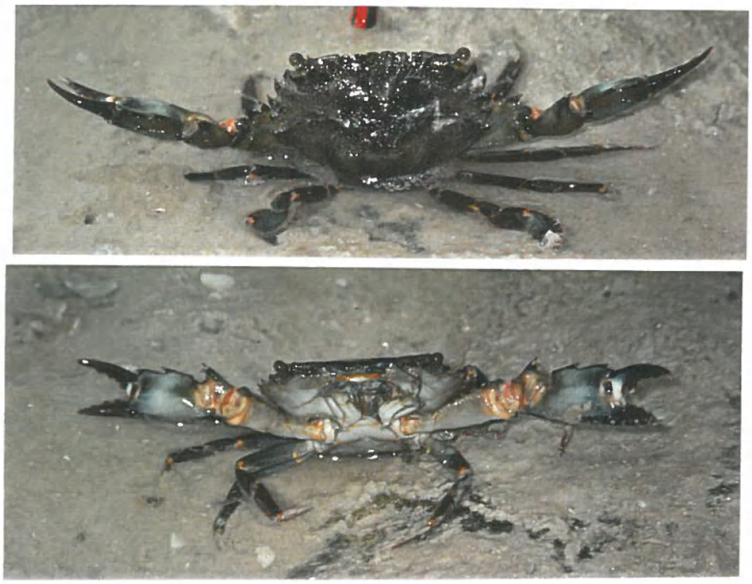


Eurycarcinus natalensis (male), Kenya

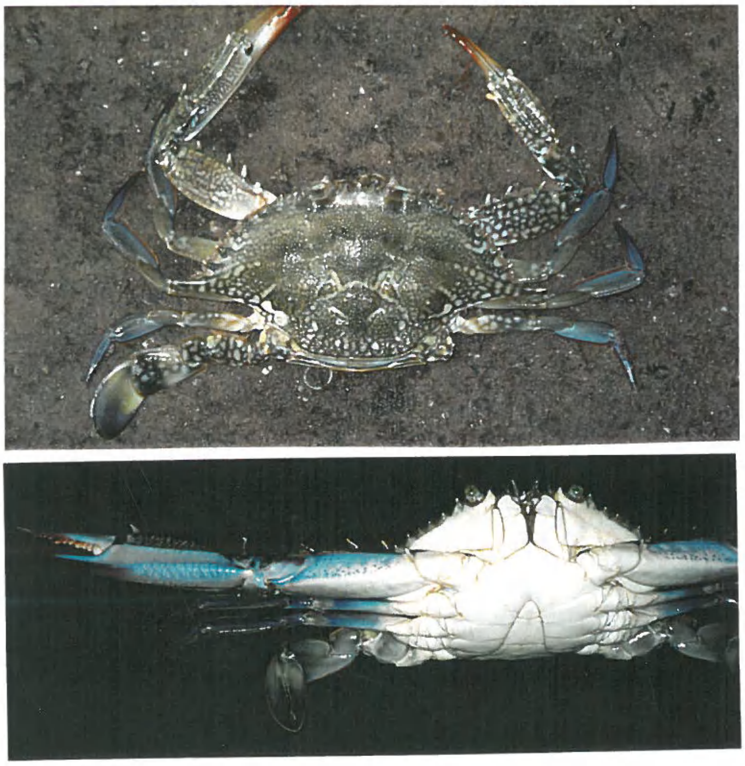
Ozius guttatus (female), Kenya

Epixanthus dentatus, Kenya

Scylla serrata, Mozambique



Thalamita crenata (male), Kenya



Portunus pelagicus, Kenya

Cardisoma carnifex (female)
Kenya

Metopograpsus oceanicus (female)
Kenya, mm 28.6 x 22.9

Metopograpsus thukuhar (male)
Kenya, mm 23.0 x 17.8

Neosarmatium meinerti (male)
Kenya, mm 32.0 x 30.0

Neosarmatium meinerti (male)
Kenya, mm 32.0 x 30.0

Sesarma guttatum (male)
Kenya, mm 18.5 x 14.8

Sesarma guttatum (male), Mozambique

Sesarma ortmanni (female)
Kenya, mm 19.9 x 15.2

Sesarma leptosoma (male)
Kenya, mm 25.2 x 17.2

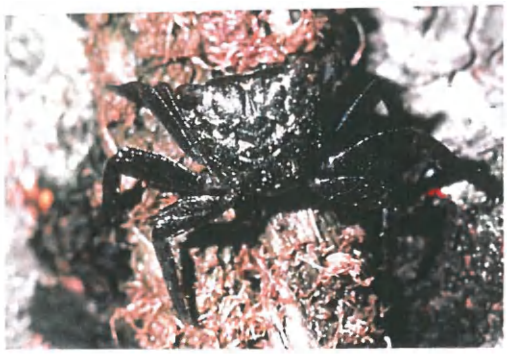
Sesarma villosum (female)
Kenya, mm 11.7 x 10.0

Sesarma longipes (male)
Kenya, mm 18.8 x 14.4

Selatium elongatum (male)
Kenya, mm 36.0 x 34.5

Selatium brockii (male)
Kenya, mm 21.4 x 19.0

Neosarmatium smithi (male)
Kenya



Sesarma leptosoma Kenya
on roots and among *Rhizophora* leaves.
Particular : traces of the crab feeding on leaves.

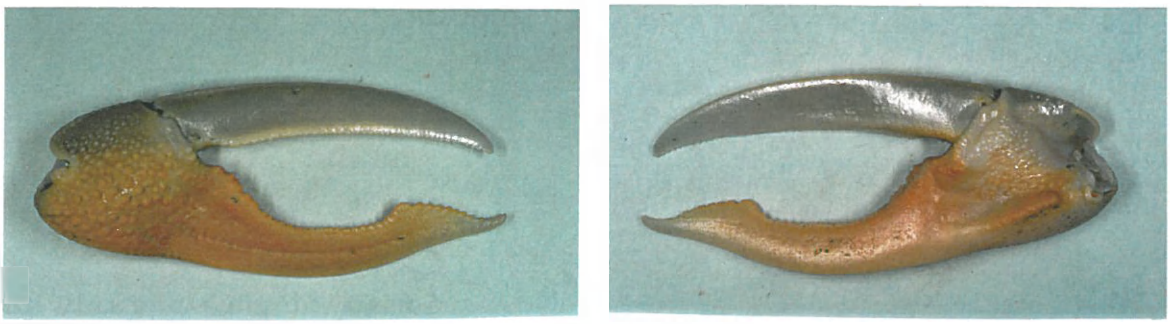
Neosarmatium meinerti (male)
Kenya

Sesarma ortmanni (male)
Kenya

Metopograpsus thukuhar (male), Kenya

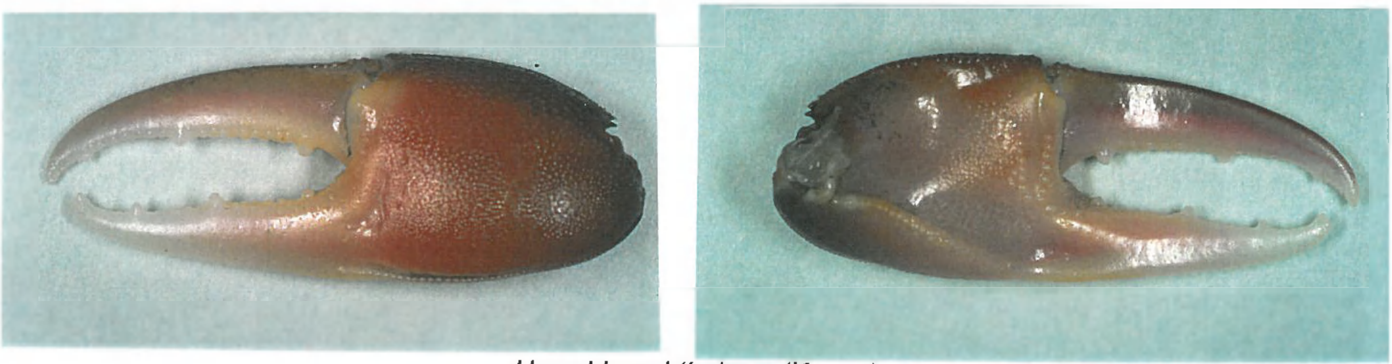
Sesarma catenata (male)
Mozambique

Grapsus fourmanoiri (male), Kenya

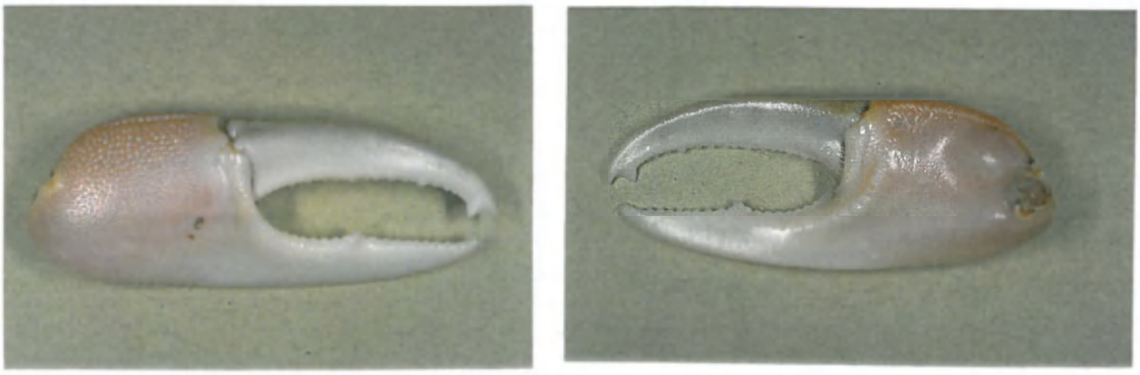


Uca vocans hesperiae (Kenya)

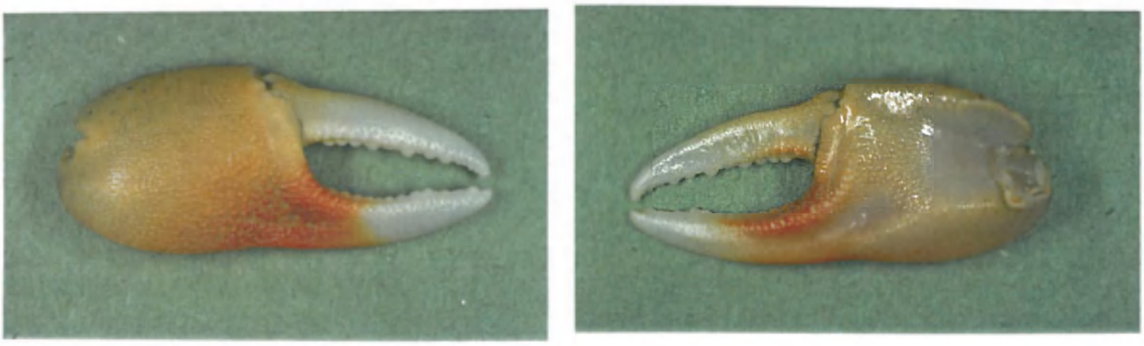
Uca annulipes (Kenya)



Uca chlorophthalmus (Kenya)



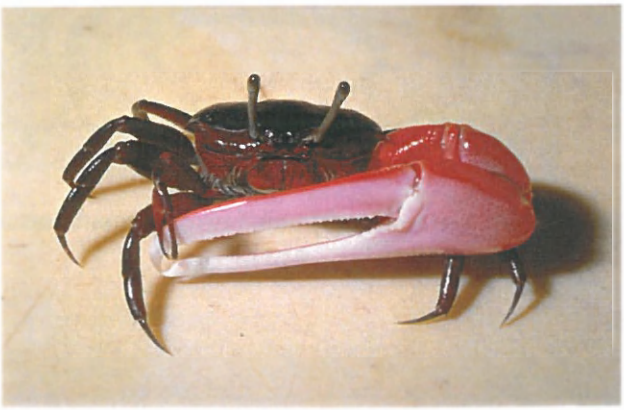
Uca inversa (Kenya)



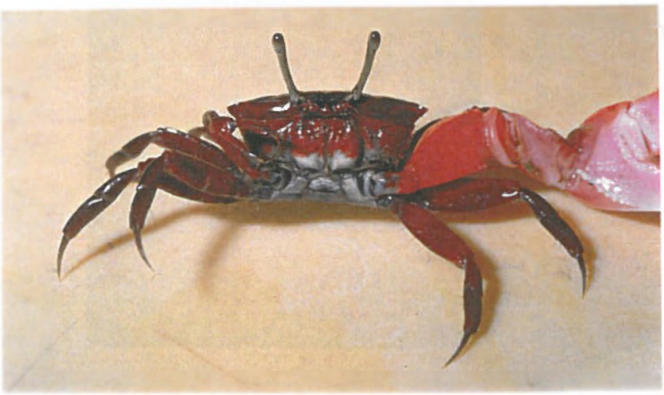
Uca tetragonon (Kenya)

Uca urvillei (male), Mozambique

Uca urvillei (male), Kenya



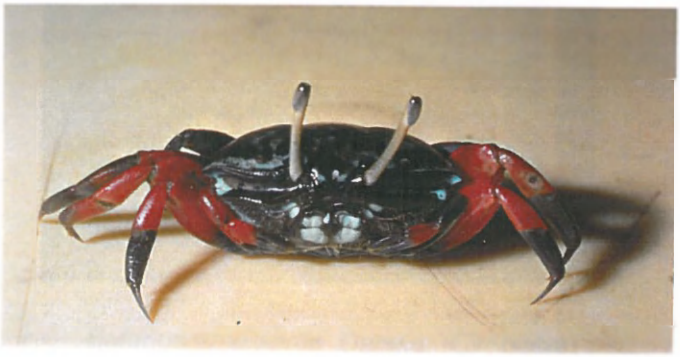
Uca annulipes (male), Mozambique



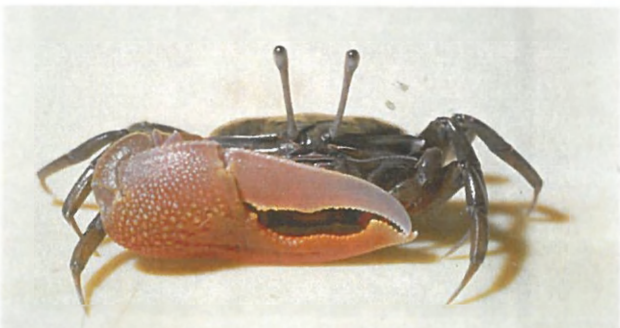
Uca annulipes (male), Mozambique

Uca urvillei (male), Mozambique

Uca chlorophthalmus (male and female), Mozambique



Uca chlorophthalmus (female), Mozambique



Uca vocans hesperiae (male), Mozambique

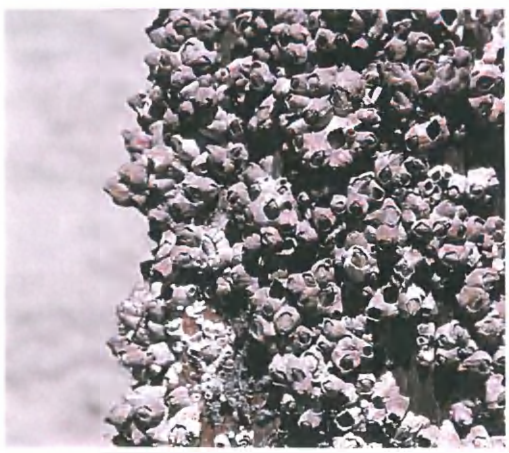
Ocypode ceratophthalmus (Ocypodidae)
Kenya

Macrophthalmus grandidieri (Ocypodidae), female
Kenya

Dotilla fenestrata (Ocypodidae)
Kenya

Clibanarius laevimanus (Anomura, Diogenidae)
a cluster of thousands of individuals on a dead
Sonneratia alba

Balanus amphiprite Darwin (Cirripedia)



Cthamalus dentatus (Cirripedia)

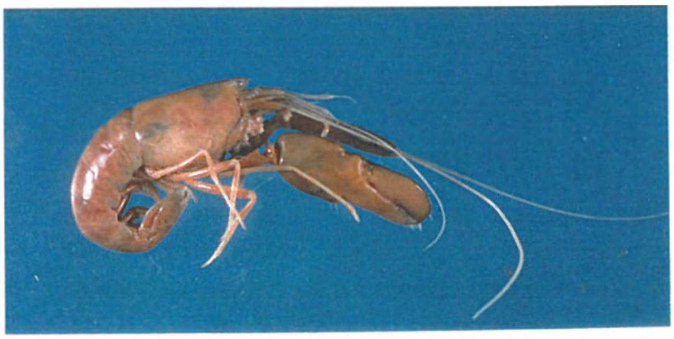
Coenobita cavipes, Kenya

Clibanarius longitarsus (female)
Kenya, carapace length mm 10

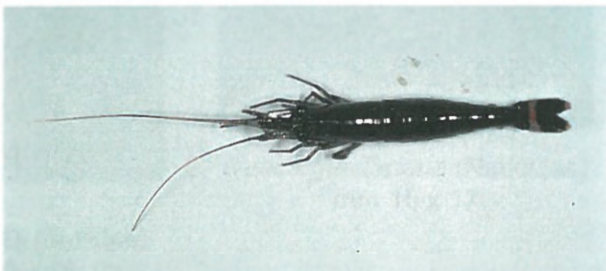
Clibanarius laevimanus (male)
Kenya, carapace length mm 41

Petrolisthes lamarckii (male)
Kenya, mm 14 x 14.2

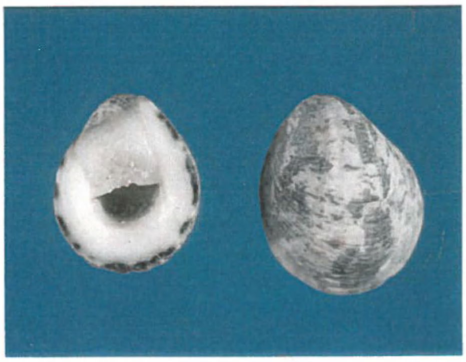
Petrolisthes lamarckii (male)
Kenya, mm 14 x 14.2



Alpheus crassimanus, Kenya



Merguia oligodon (female)
Kenya, total length mm 30



Nerita albicilla (Neritidae)
mm 12 x 15

Terebralia palustris (Cerithidae)
cluster of animals on a *Rhizophora* leaf

Littorina scabra (Littorinidae)
on a dead tree trunk

Morula granulata (Muricidae)
mm 17 x 19

Cerithium caeruleum (Cerithidae)
mm 15 x 25

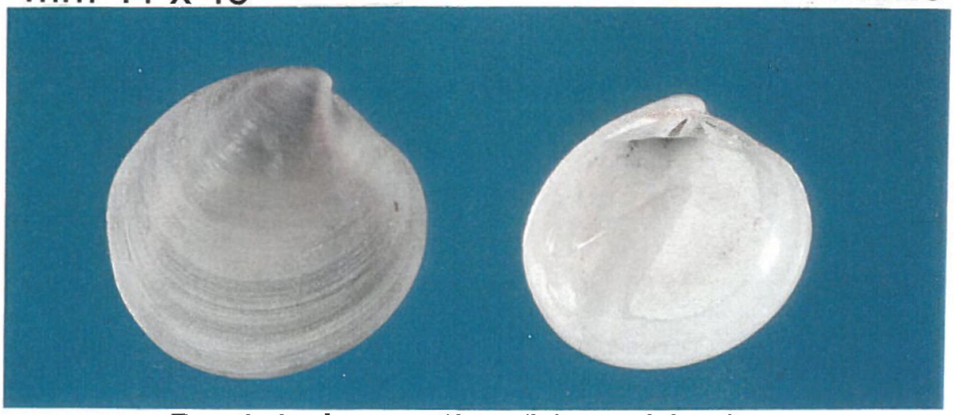
Volema paradisiaca (Melongenidae)
mm 34 x 55

Bulla ampulla (Bullidae)
mm 26 x 38

Natica gualteriana (Naticidae)
mm 15 x 17

unknown species (Arcidae)
mm 41 x 48

unknown species (Veneridae)
mm 20 x 26



Dosinia haepatica (Veneridae)
mm 17 x 18

Loripes rosacea (Lucinidae)
mm 21 x 21

unknown species (Mytilidae)
mm 8 x 15